Long-term individual foraging site fidelity – why some gannets don't change their spots

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Abstract

Many established models of animal foraging assume that individuals are ecologically equivalent. However, it is increasingly recognized that some populations comprise animals whose diets and foraging behaviours differ consistently among individuals. For example, recent studies have shown that individual foraging site fidelity (IFSF - when individuals consistently forage in only a small part of their population's home range) occurs in some colonial breeders. Short-term IFSF could result from animals using a win-stay, lose-shift (WSLS) foraging strategy. Alternatively, it may be a consequence of other forms of individual specialisation. Pelagic seabirds are colonial central-place foragers, classically assumed to use flexible foraging strategies to target widely

dispersed, spatiotemporally patchy prey. However, tracking has shown that IFSF occurs in many seabirds, although it is not known whether this persists across years. To test for long-term IFSF and to examine alternative hypotheses concerning its cause, we repeatedly tracked 55 northern gannets from a large colony in the North Sea within and across three successive breeding seasons. Gannets foraged in neritic waters, predictably structured by tidal mixing and thermal stratification but subject to stochastic wind-induced overturning. Both within and across years, coarse to mesoscale (10s km) IFSF was significant but not absolute and foraging birds departed the colony in individually consistent directions. Carbon stable isotope ratios in gannet blood tissues were repeatable within years and nitrogen ratios were also repeatable across years, suggesting long-term individual dietary specialisation. Individuals were also consistent across years in habitat use with respect to relative sea surface temperature and in some dive metrics yet none of these factors accounted for IFSF. Moreover, at the scale of weeks, IFSF did not decay over time and the magnitude of IFSF across years was similar to that within years, suggesting that IFSF is not primarily the result of WSLS foraging. Rather, we hypothesise that site familiarity, accrued early in life, causes IFSF by canalising subsequent foraging decisions. Evidence from this and other studies suggests that IFSF may be common in colonial central-place foragers, with far-reaching consequences for our attempts to understand and conserve these animals in a rapidly changing environment.

Keywords: Site familiarity, individual specialisation, niche partitioning, gannet, *Morus bassanus*, GPS tracking, central-place forager, tidal mixing front.

Introduction

An assumption implicit to many established theories of animal habitat selection, such as the ideal free and ideal despotic models (Fretwell and Lucas 1969), is that individuals are ecologically equivalent (Piper 2011). Hence, the increasing realisation that behaviour in many animal populations differs consistently among phenotypically similar individuals has far reaching implications for ecology, evolution and wildlife management (Bolnick et al. 2003, Piper 2011, Dall et al. 2012). Site fidelity (when an animal repeatedly uses the same location) is a common form of individual behavioural consistency (Switzer 1993, Piper 2011). For example, birds frequently return each year to the same breeding territory or wintering area (Phillips et al. 2005, Piper 2011). Similarly, individual foraging site fidelity (IFSF) occurs when within-individual variation in the use of space during foraging is less than that across the population as a whole. As such, IFSF could be regarded as a form of individual specialisation (Bolnick et al. 2003, Patrick et al. 2014). However, IFSF could be either a cause or a consequence of other types of specialisation (e.g. in diet, behaviour, habitat, etc.) (Woo et al. 2008, Beverly et al. 2009) or it could have other, unrelated, proximate causes (Piper 2011). In colonial animals, theory suggests that the individual behaviour is influenced by that of the group (Ward and Zahavi 1973). It is perhaps surprising therefore that recent studies have shown IFSF in breeding seabirds and other colonial central-place foragers, including pinnipeds, bats and ants (Kerth et al. 2001, Weimerskirch 2007, Beverly et al. 2009, Baylis et al. 2012). Although individual dietary and behavioural specialisation is frequent in seabirds (Patrick et al. 2014), there is little evidence on the causal relationships between these phenomena and IFSF. Moreover, it is unknown whether IFSF in seabirds persists across breeding seasons (Weimerskirch 2007).

IFSF could also be a consequence of search behaviour. In a spatiotemporally patchy environment, foragers may employ a win-stay, lose-shift (WSLS) strategy (Kamil 1983, Davoren et al. 2003). If this were the case, IFSF would continue only for as long as prey patches persisted but would ultimately decay over time. Classically, pelagic seabirds were assumed to forage on highly patchy and unpredictable resources, making them necessarily flexible foragers, reliant largely on searching or public information gain, rather than memory, to locate their prey (Lack 1968, Ward and Zahavi 1973). However, recent observations that IFSF within breeding seasons is high, and that birds travel directly to foraging areas, rather than following sinuous search paths, has been regarded as evidence that the occurrence of prey (in temperate and polar seas at least) is predictable at the coarse- to mesoscale (10s – 100s km) and over days and weeks (Irons 1998, Weimerskirch 2007). However, the swarming species upon which seabirds principally prey are likely distributed in a hierarchical patch system, in which predictability reduces with decreasing spatiotemporal scale (Fauchald and Tveraa 2006). This is evinced by the fact that some species use nested area restricted search (ARS) patterns, the scale of which is matched to that of habitat structures (Pinaud and Weimerskirch 2005, Hamer et al. 2009). Moreover, seabird breeding success, which is dependent largely on food supply, varies markedly between years (Cury et al. 2011). As such, it may be advantageous for seabirds to maintain sufficient behavioural plasticity to respond to environmental stochasticity, for example by using public information to locate new prey patches and private information (memory) to relocate them (Ward and Zahavi 1973, Weimerskirch et al. 2010, Wakefield et al. 2013). Hence, if IFSF is attributable to WSLS foraging, then its rate might be expected to match the scale of environmental variability and decay over time. Moreover, if repeatability in diet, habitat choice and prey capture method are consequences rather than causes of IFSF, then individual

93 specialisations might also be expected to decay over time. This prediction is consistent with the
94 observation that rates of behavioural repeatability tend to be higher when observations are
95 closely spaced (Woo et al. 2008, Bell et al. 2009) but contrary to the observation that individual
96 dietary specialisations persist over inter-annual scales in some wide-ranging higher marine
97 predators (Matich et al. 2011, Vander Zanden et al. 2013).
98
99 Irons (1998) suggested an alternative cause of IFSF: site familiarity. That is, by maintaining
100 foraging site fidelity seabirds acquire information specific to that site, such as local tidal features,
101 conferring a competitive advantage (the 'always stay' strategy (Switzer 1993)). Until recently
102 site familiarity has received little attention yet it may play an important role in habitat selection
103 by making animals more spatially conservative with experience (Piper 2011). If seabirds'
104 foraging decisions are affected by site familiarity then IFSF may persist across breeding seasons.
105 Inter-annual IFSF has been recorded in breeding pinnipeds (Bradshaw et al. 2004, Call et al.
106 2008). However, to our knowledge, no previous studies have tested for it in breeding seabirds or
107 examined the relationship between IFSF and other forms of individual behavioural consistency at
108 this scale (Weimerskirch 2007, Patrick et al. 2014). Moreover, the fitness consequences of IFSF
109 and individual specialisation are far from clear (Woo et al. 2008).
110
111 Northern gannets *Morus Bassanus* (hereafter gannets) are large pelagic seabirds that breed on
112 temperate to low-Arctic coasts of the North Atlantic (Nelson 2001). They range up to 100s km
113 from their colonies to forage almost exclusively in neritic waters (Hamer et al. 2000, Garthe et
114 al. 2011, Wakefield et al. 2013). Breeding individuals tracked for up to 3 weeks show significant
115 but not absolute IFSF (Hamer et al. 2001, Patrick et al. 2014). Moreover, they tend to follow

highly directed paths from their colonies, supporting the hypothesis that they anticipate the location of their prey at the timescale of days-weeks and scales of 10s to 100s of km (Pettex et al. 2010). However, at finer scales (10s km) they also use ARS, which is characterised by a tortuous flight path (Fauchald and Tveraa 2006), to locate prey, though it is not known whether the scale of ARS reflects that of prey patches or underlying habitat structures (Hamer et al. 2009). At these scales they also gain information on prey distribution from observing foraging conspecifics (local enhancement) (Camphuysen 2011) and may be attracted to fishing vessels, from which some individuals obtain large quantities of discards (Votier et al. 2010, Bodey et al. 2014). Gannets capture prey by diving, following either V or U-shaped profiles depending on prey type (Garthe et al. 2000). Blood tissue stable isotope ratios indicate that individuals are short-term dietary specialists (Kakela et al. 2007, Votier et al. 2010), while consistent differences in individual behavioural responses to sea surface temperature (SST), chlorophyll-a and copepod abundance have been interpreted as evidence of site specialisation (Patrick et al. 2014).

Gannets breeding at the Bass Rock in the North Sea, one of the world's largest colonies (~60,000 breeding pairs), forage in habitats that are predictably structured at the coarse to mesoscale (10s – 100s km) by the tide and seasonal thermal stratification (Fig. 1). Shallower waters remain mixed due to tidal stirring, with tidal mixing fronts forming at the interface of these two regimes (Simpson 1981). Such tidally forced dynamics are very predictable. However, both seasonal stratification and the location of mixing fronts is subject to modification by wind-induced overturning, which is episodic and unpredictable within breeding seasons, and tracking data show that population level home ranges can vary considerably across years, presumably in response to variability in prey availability (Hamer et al. 2007).

Despite this wealth of information, it is not known whether IFSF occurs across breeding seasons or whether individual specialisations persist at this scale. The aims of our study were therefore, first, to determine whether IFSF in a colonial central-place forager inhabiting a patchy but semi-predictable environment persists over long time scales and, second, to examine the potential causes of IFSF. By repeatedly tracking and blood-sampling the same individual gannets from Bass Rock within successive breeding seasons we tested (at the scale of weeks and years) the hypotheses that IFSF: (1) is significant and dependent on consistency in diet, foraging behaviour or habitat use; (2) decays over time; (3) varies with the directedness of trips, and; (4) affects individual body condition.

Materials and Methods

Study design and data collection

Fieldwork was conducted on Bass Rock (56° 6'N, 2° 36'W, Fig. 1) from June - August, 2010 – 2012, during which time we collected blood samples from adult gannets and tracked their movements over successive foraging trips. We aimed firstly to estimate individual consistency (defined below) in the use of space and habitat in a comparable manner within years and across years. We therefore aimed to track birds for a minimum of three foraging trips within each of three consecutive breeding seasons. In the event, we were able to track some birds for > three trips within years (see Results). Where possible, we analysed these additional data using hierarchical models.

Birds of unknown age were caught at the nest, while they were attending 2 - 5 weeks old chicks, using a metal crook or brass wire noose fitted to a 4-6 m telescopic pole, and restrained in a custom-made jacket. Time permitting, on initial capture we measured culmen length (tip to feathering) and maximum tarsus length (± 1 mm) using a Vernier calliper. On first capture within each year, *y* (time $t_{y,1}$), after birds had fed their chicks, we also measured body mass to the nearest 25 g using a 5 kg spring balance. We then attached an Igotu GT-200 or GT-600 (Mobile Action Technology Inc., Taipei, Taiwan, 37 g) Global Positioning System (GPS) logger to the dorsal side of the central three tail feathers using Tesa tape. GPS units sampled position at 2 minute resolution. In addition, in 2011 and 2012, we fitted some birds with a Time Depth Recorder (TDR; either a G5, CEFAS Technology, Lowestoft, UK or MSR145, MSR Electronics GmbH, Seuzach, Switzerland, 2.5 g and 18 g respectively). Birds were recaptured (time $t_{y,2}$), and loggers removed after 1 – 3 weeks. Total instrument mass was d 2% of body mass, below the maximum recommended for bio-logging studies (Phillips et al. 2003). After release, birds returned almost immediately to the nest, and devices had no discernible effects on birds' trip durations (Cleasby et al. in press).

At both $t_{y,1}$ and $t_{y,2}$ we collected ~ 0.8 ml of blood from the tarsal vein of each gannet using a 23 gauge needle (under a UK Home Office licence). Within an hour, we centrifuged samples at 15,000 rpm for 10 minutes to separate plasma and erythrocytes, which were then stored frozen. In addition, we retained 0.2 ml of whole blood from each bird, which we stored in 98% ethanol for molecular sex determination, which was carried out at the Natural Environment Research Council (NERC) Biomolecular Analysis Facility, Sheffield. Throughout the study, we collected,

identified and stored prey spontaneously regurgitated by adult gannets during handling to assess their diet (Votier et al. 2010).

To describe the distribution and consistency of individual foraging effort with respect to habitat, we considered environmental variables known to influence the distribution of foraging gannets or their prey. These variables, and our rationale for selecting them, were: (i) Distance from colony: The energetic and temporal costs of foraging as well as the intensity of intraspecific competition vary with distance from the colony (Wakefield et al. 2013); (ii) depth and (iii) slope of seafloor: Gannets sometimes forage over relatively shallow offshore banks, which are an important habitat for sandeels *Ammodytes* spp., which comprise up to half of the biomass in the diet of gannets at Bass Rock in some years (Hamer et al. 2007), as well as areas of steep bathymetric relief (Hamer et al. 2001, Scott et al. 2010); (iv) fishing effort: Fishery discards comprise ~ 10 – 30 % of the diet of gannets in UK waters (Hamer et al. 2007, Kakela et al. 2007, Votier et al. 2010) and foraging gannets are attracted to fishing vessels (Votier et al. 2010, Camphuysen 2011, Bodey et al. 2014); (v) SST and (vi) relative front density (Miller 2009): In shallow, tidally dominated seas, SST discriminates thermally stratified (warm) from tidally mixed (cool) waters (Simpson 1981). The density of foraging gannets varies systematically with SST (Scott et al. 2010) and increases in the vicinity of tidal mixing fronts between cool and mixed waters (Hamer et al. 2009); (vii) Net Primary Production (NPP): The distribution of mesotropic fish that gannets prey upon (e.g. mackerel *Scomber scombrus* and herring *Clupea harengus*) is partly limited by lower trophic level organisms, for which NPP is a proxy. The density of foraging gannets therefore tends to increase with primary production (Grémillet et al.

2008, Scott et al. 2010, Votier et al. 2010). For sources and pre-processing of environmental data see Appendix A.

Quantifying repeatability

Individual consistency in continuous measures of behaviour or diet may be quantified using the repeatability, *R*, where

$$R = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2}, \quad (1)$$

and σ_{α}^2 and σ_{ε}^2 is the variance between- and within individuals respectively. This index and its implementation are discussed at length by Nakagawa and Schielzeth (2010). The variance components in eq. 1 may be estimated using linear mixed-effects models of the variable of interest as a function of animal identity, which is specified as a random effect. Other explanatory terms (e.g. sex, age, etc.) can be included as fixed effects. In this case, Nakagawa and Schielzeth (2010) use the term adjusted repeatability R_{adj} because controlling for fixed effects will affect the variance component (and hence repeatability) estimates in equation 1. By implementing these models in a Bayesian framework, posterior estimates can be used to calculate credibility intervals around R_{adj}. Following this approach, we used the R package MCMCglmm (Hadfield 2010) to model behavioural and dietary indices using generalised linear mixed-effects models (GLMM) fitted to all trip data. We simplified models by backward-selection, minimising the Deviance Information Criterion (*DIC* (Claeskens and Hjort 2008)) and retaining fixed effects only if their removal resulted in an increase in *DIC* of 5 or more (Lunn et al. 2012).

In order to examine the relationship between individual repeatability and other covariates we also calculated the individual-level adjusted repeatability for each bird:

$$R'_{adj,i} = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_i^2}, \quad (2)$$

where σ_α^2 is the between-individual residual variance component and σ_i^2 is the residual variance for the *i*th individual, estimated by the minimum adequate model.

Isotopic repeatability

In order to estimate individual dietary repeatability (hypothesis 1), we used the ratios of stable isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) in the blood tissues of birds (expressed as $\delta^{15}N$ and $\delta^{13}C$ respectively) as proxies for diet (Appendix B for further details). $\delta^{15}N$ values vary with the trophic position of prey and $\delta^{13}C$ values with water mass, depth and distance from land (Hobson et al. 1994, Cherel and Hobson 2007). Due to their different turnover rates, body tissues integrate diet at different time scales. The half-lives of both stable isotope ratios in avian blood plasma (PLA) and red-blood cells (RBC) range from approximately 1 - 8 days and 14 - 30 days, respectively (Barquete et al. 2013). The repeatability of stable isotope ratios in different tissues collected from an individual at the same time or the same tissues collected at different times is therefore a proxy for individual dietary specialization (Bearhop et al. 2006, Matich et al. 2011). Accordingly, blood samples were collected from each gannet at $t_{y,1}$ and $t_{y,2}$ and separated into plasma and erythrocytes, if possible, in each study year. Sex was determined using molecular

methods. Prey and gannet tissue samples were prepared following standard procedures and stable isotope ratios measured by continuous flow mass spectrometry (Appendix B for details).

We estimated R_{adj} and R'_{adj} for δ^{15}N and δ^{13}C in the blood tissues of gannets, within and across years. Within each year, we modelled isotopic ratios in RBC and PLA sampled at $t_{y,1}$, and PLA sampled at $t_{y,2}$ as repeated measures. Across years, we modelled isotopic ratios in RBC sampled at $t_{y,1}$ in each year. Exploratory data analysis showed stable isotope values to be approximately normally distributed. We considered the following candidate fixed effects: (i) sex (diet, spatial usage and foraging behaviour of male and female gannets differ (Lewis et al. 2002, Stauss et al. 2012, Cleasby et al. in press)); (ii) tissue type (enrichment of δ^{13}C and δ^{15}N tends to differ systematically with tissue type (Zhao et al. 2006)); (iii) environmental baseline δ^{13}C and δ^{15}N (Jennings and Warr 2003, Barnes et al. 2009). (In the marine environment, differing rates of primary productivity can result in spatial variation in baseline stable isotope ratios (Moreno et al. 2011). Baseline δ^{15}N is 2 to 2.5 ‰ higher in the permanently mixed waters of the southern North Sea than in the northern sector (Fig. 2 in Jennings and Warr 2003), while that of δ^{13}C is 0.5 to 1 ‰ higher (Fig. 2 in Barnes et al. 2009). In addition, δ^{13}C decreases with distance from the coast. Hence, repeatability in gannet tissue isotopic ratios may reflect not only dietary repeatability but spatial consistency.); (iv) year (baseline stable isotope ratios may change from year to year (Moreno et al. 2011)). Random effects allowed for among-individual variation in intercepts the response baseline stable isotope ratios.

We obtained baseline estimates of δ^{15}N and δ^{13}C from isoscapes predicted by models fitted to tissue isotope ratios measured in phytoplankton-feeding bivalve molluscs (*Aequipecten*

opercularis) sampled throughout the North Sea (Jennings and Warr 2003, Barnes et al. 2009). We digitised isoscapes presented in these publications and appended baseline ratios to each tracking location. For each bird, we then calculated the median baseline isotopic ratio across all putative foraging locations within each year (Appendix B for details).

Behavioural repeatability

To test hypotheses 1 and 4, we summarised individual foraging behaviour by trip using the following indices (Appendix C for details): daylight trip duration, assuming that this reflects available foraging time; median foraging range; ARS scale (i.e. the scale at which variance in the first-passage time peaked (Pinaud and Weimerskirch 2005)). For birds equipped with TDRs we also calculated the mean dive depth, mean maximum dive depth, dive rate, and the proportion of V shaped dives (dives were classified as either V-shaped or U-shaped), all of which potentially reflect individual differences in foraging strategies, prey types or habitat use (Garthe et al. 2000, Woo et al. 2008). We estimated R_{adj} and R'_{adj} of these indices by treating trips as individual-level repeated measures, within or across years and considering sex and in the latter case, year, as candidate fixed effects. We $\log_e$-transformed trip duration and ARS scale and square-root-transformed foraging range to improve normality and assumed binomial errors for the proportion of U-shaped dives and Poisson errors for dive rate.

Quantifying spatial and environmental consistency

To test hypotheses 1 - 4, we quantified individual consistency in departure directions, coarse to mesoscale (10s km) space use and habitat use. Following Wakefield et al. (Wakefield et al. 2013) we first used movement metrics to identify putative foraging bouts (Appendix C for details).

294 Validation of this approach against known dive locations recorded using TDRs has shown that
295 99% of GPS locations occurring within 10 minutes of known dive locations are classified as
296 foraging. Conversely, 62% of GPS locations classified as foraging occur within 10 minutes of
297 known dives (Wakefield et al. 2013) (note that gannets frequently exhibit search behaviour
298 without diving (*35*)). We then matched the most spatiotemporally proximate value of each
299 environmental index to each foraging location. In order to describe foraging consistency with
300 respect to relative, rather than absolute environmental covariates, we also considered dynamic
301 covariates standardised by subtracting the mean and dividing by the standard deviation.
302
303 We adopted a simple technique, based on the utilisation distribution (UD), to estimate foraging
304 consistency. UDs quantify not only which locations an animal uses but what proportion of their
305 time they spend in each (Fieberg and Kochanny 2005) and may also be used to describe usage in
306 environmental space. We estimated the foraging UD in Cartesian space ($\hat{UD}_{i,j}(x,y)$) of each
307 individual *i*, during its *j*th trip as follows: We first projected foraging locations (longitude and
308 latitude) onto a Lambert equal area projection (*x*,*y*) grid. We then estimated their kernel density
309 using the R package 'adehabitat' (Calenge 2006), specifying a bivariate normal kernel, a fixed
310 bandwidth (*h*) of 15 km and a grid resolution of 16 km. We quantified within-individual
311 consistency in the use of space and habitat by calculating the overlap between UDs of multiple
312 trips using Bhattacharyya's affinity (Fieberg and Kochanny 2005), which ranges from 0 (no
313 similarity between UDs and therefore no spatial consistency) to 1 (identical UDs/perfect spatial
314 consistency). In Cartesian space the overlap between the first and second trips made by the *i*th
315 bird is:
316

317 $$\beta_{x,y,i} = \sum_{x,y} \sqrt{\hat{UD}_{i,1}(x,y)\hat{UD}_{i,2}(x,y)} \quad (3)$$

318

319 Similarly, to estimate individual consistency with respect to habitat we estimated β_i in each

320 dimension *k* of environmental space (SST, NPP, etc.) by substituting $\hat{UD}_{i,j}(k)$ for $\hat{UD}_{i,j}(x,y)$ in

321 equation 3. We estimated trip kernel density in the *k*th dimension of environmental space (UD$k_{i,j}$)

322 using the R 'stats' package (Venables and Ripley 2002). In order to define *h* for environmental

323 indices we determined *h* for each using Scott's rule (Scott 1992).

324 We quantified individual-level behavioural consistency at two temporal scales: Within-year, we

325 calculated the mean Bhattacharyya's affinity $\hat{\beta}_i$ of all pairwise combinations of the first three

326 trips recorded. Across years, we calculated $\hat{\beta}_i$ of all pairwise combinations of the first trips

327 recorded in each study year (Fig. 1). We then calculated the population mean consistency $\overline{\beta}$.

328 Hence, $\overline{\beta}$ is based three trips per sampling scale (within or across breeding seasons) making its

329 magnitude is comparable across scales.

330

331 In itself, $\overline{\beta}$ is not particularly informative because it reflects both population and individual

332 consistency and cannot therefore be compared directly across usage dimensions. Rather, we used

333 a randomisation procedure to test the null hypothesis that within-individual consistency in each

334 dimension is greater than population-level consistency. If the null hypothesis is correct, then

335 observed consistency should not differ significantly from that when bird identity is randomly

336 assigned. We estimated the null distribution of $\overline{\beta}$ by randomly reassigning bird identities to trips,

337 either within or across years, without replacement and recalculating $\overline{\beta}$ and $\overline{\rho}$. To avoid sex-

specific behaviour (Stauss et al. 2012) inflating null estimates of this statistic, bird identities were reassigned within sexes. Similarly, trips from different birds made at the same time might be expected, *a priori*, to be more similar than those made at different times. To avoid this potentially inflating our null estimate of $\overline{\beta}$, we reassigned bird identity such that trip order was preserved. For each period, we used 999 permutations. $\overline{\beta}$ cannot be less than the null so we treat this as a one-tailed test.

To test hypotheses 1, 3 and 4 we also quantified individual consistency in departure directions. Variation in the flight direction of gannets relative to the colony diminishes rapidly with colony distance (Pettex et al. 2010). Hence, we defined departure direction as the circular average of the bearing from the colony to the first five locations >10 km from the colony (Patrick et al. 2014). For the *i*th individual, we then estimated directional consistency using mean resultant length $\hat{\rho}_i$ of departure directions, which ranges from 0 (no directional consistency) to 1 (all directions equal). We estimated $\hat{\rho}_i$ across three foraging trips. Within years, departure directions were those of the first three trips recorded in that year and across years, those of the first trip recorded in each year (for examples, see Appendix D). We then calculated the population-level mean directional consistency, $\overline{\rho}$ and tested whether this was significantly greater than the null expectation using the randomisation procedure described above. In order to check whether the trip selected affected our conclusions with respect to consistency across years we repeated inter-annual analysis ten times randomly selecting trips birds.

To test whether directional and spatial consistency within years decayed exponentially over time, we calculated ρ and $\beta_{x,y}$ between pairs of trips separated by different lags, *l*, where *l* is the difference in trip number. We then calculated the within-individual mean $\hat{\rho}'_{l,i}$ and $\hat{\beta}'_{x,y,l,i}$ and modelled these indices a function of *l*, using binomial GLMs and specifying random slopes and intercepts for individuals. We used likelihood ratio tests to determine whether these models explained the data any better than the respective intercept-only models. To test whether directional and spatial consistency declined over successive years, within individuals, we also calculated ρ and $\beta_{x,y}$ between the first trips recorded in 2010 and 2011 and 2010 and 2012.

Directedness of trips

The two-dimensional shape of pelagic seabird foraging trips falls on a spectrum between highly linear and highly circuitous (Weimerskirch 2007). To test hypothesis 3, we therefore devised a simple index ^{o} to quantify the linearity of each trip, which varies between 0 (track describes a circle, with diameter equal to the maximum distance reached from the colony) and 1 (track perfectly linear; Appendix C for further details). For each individual *i* we calculated $\hat{\kappa}_i$, the mean linearity across trips 1-3 within years and across the first trip recorded in each study year. We then tested the Spearman rank correlation coefficient (r_s) between $\hat{\kappa}$ and indices of foraging repeatability and consistency.

Effects of consistency on body condition

In order to quantify between-individual variation in body condition we first tested the dependence of body mass on sex (females are heavier than males (Stauss et al. 2012, Cleasby et al. in press)), culmen length and tarsus length (Votier et al. 2010), using mixed-effects linear

models. Most birds were weighed repeatedly across years so individual was specified as a random effect. Assuming this to be the maximal model, we tested the hypotheses that successively simpler models differed from one another using likelihood ratio tests. We assume that residual body mass predicted by the covariates retained varies with body condition. We tested whether this was dependent on individual consistency, repeatability or trip linearity using simple linear models. Not all indices of consistency and repeatability were available for all birds in all years. Hence, to maximise sample sizes, we fitted separate models for each period.

Covariance between consistency and repeatability

To determine whether birds that are spatially consistent are also consistent in their use of habitat, we calculated the Spearman rank correlation r_s between spatial and environmental consistency. We used correlation tests to determine whether birds' consistency with respect to space and habitat use covaried with their behavioural or isotopic repeatability. To determine whether birds with narrow diets also forage in a particular manner, we also calculated the correlation between individual isotopic repeatability, behavioural repeatability and consistency with respect to space and habitat. These procedures involved multiple comparisons, so we used the Bonferroni correction to adjust the level of significance to ± = 0.05/n, where n is the number of correlation tests applied in each case. Throughout the rest of the analysis significance was set at ± = 0.05. Unless otherwise stated, medians are quoted with their inter-quartile range (IQR) and means with their 95% confidence intervals.

Results

We GPS-logged e 3 consecutive foraging trips from 37, 20 and 31 birds in 2010, 2011 and 2012, respectively, with up to 12 trips per bird in 2010, 14 in 2011 and 7 in 2012. However, some individuals were tracked in only one or two breeding seasons or for <3 trips per season (see Table E1 for details). Birds foraged significantly closer to the colony in 2011 (median distance 109, IQR 65 - 175 km) than in 2010 and 2012 (175, 108 - 178 and 160, 97 - 242 km respectively; Fig. 2, Fig. F1, Table E2).

Environmental conditions, variability and fisheries

At the coarse to mesoscale, variation in the physical oceanography of waters accessible to birds from Bass Rock during the study period was relatively low but greater within than across years (Fig. F2, Table E3). The tidal mixing front separating mixed and stratified waters east of Scotland was ~ 30 km closer inshore in 2011 than in 2010 and 2012 (Fig. 1). However, there was little discernible spatial pattern in inter-annual variability in front density or NPP, indicating that these features of the environment were largely predictable at this scale. Mean fishing effort from 2007 – 2010 was concentrated: in areas <50 km from the coast to the north and south of Bass Rock, characterised by steep bathymetric relief; over relatively shallow banks (<100 m), offshore, to the east and south east; in the southern Moray Firth, and; in waters north of the 100 m isobath, to the northeast of Scotland (Fig. F3).

Diet and isotopic repeatability

Mackerel *Scomber scombrus* were the most abundant species in regurgitates obtained from gannets returning to the colony in all study years, with clupeids (*Sprattus sprattus* and *Clupea harengus*) the next most abundant (Table E4). Additionally, sandeels (*Ammodytes spp.*), one

garfish *Belone belone* and one langoustine *Nephrops norvegicus*, were recorded in 2011. The median interval between blood-sampling gannets at $t_{y,1}$ and $t_{y,2}$ was 10 days (IQR 9 – 16 days). During all periods blood tissue isotopes varied with tissue type (Table E2). At the inter-annual scale it also varied with year. Baseline environmental isotope levels had little effect on blood tissue isotopes, while sex had significant effects (on $\delta^{13}C$) only at the inter-annual scale. The isotopic signatures of different prey species recovered from regurgitates were poorly resolved (Fig. F4). However, the adjusted repeatability of $\delta^{15}N$ in the blood tissues of individuals (R_{adj} = 0.20 – 0.35) was significant both within and across years, but only marginally so within 2010 (Table 1, Table E5). The adjusted repeatability of $\delta^{13}C$ in blood tissues was significant in 2010 and 2011 but not significant in other periods.

Spatial and directional consistency

Gannets tended to depart the colony in directions and forage in areas that were individually consistent, not only within but also across years (Fig. 3, Fig. F5). Mean spatial and directional consistency ($\overline{\beta}_{x,y}$ and $\overline{\rho}$) were significantly greater than the null expectation and were similar within and across years (Fig. 4, Table E6). The method of selecting trips had little effect on our estimates of inter-annual consistency (Table E7). The limited number of gannets that we were able to observe for >3 trips within years exhibited some among-individual variability in spatial consistency. Although the majority of birds remained consistent with time a few individuals were highly inconsistent (Fig. 5). However, within years, we found no significant decay in population mean individual directional or spatial consistency with increasing lag *l* between trips (Fig. F6, Table E8). Moreover, individual directional consistency between the first trip in years 1 and 2 did not differ significantly from that between the first trip in years 1 and 3 (median $\hat{\rho}$, 2010 vs.

2011 = 0.99, IQR = 0.98 – 1; 2010 vs. 2012 = 0.99, IQR = 0.98 – 1; paired Wilcoxon signed-rank test $V = 75$, p = 0.744, n = 16). Similarly, individual spatial consistency did not differ between these periods (median $\hat{\beta}$, 2010 vs. 2011 = 0.32, IQR = 0.24 – 0.44; 2010 vs. 2012 = 0.40, IQR = 0.26 – 0.51; paired Wilcoxon signed-rank test $V = 64$, p = 0.860, n = 16).

Environmental consistency

Individuals foraged at consistent distances from Bass Rock, both within and across years (Fig. 4). Individual consistency was highest in 2011 but did not differ from the null expectation, presumably because population level variability in foraging range was low in that year. In all other periods consistency was significant. Gannets foraged both in productive, mixed, inshore waters and less productive, thermally stratified, offshore waters but usage was highest in the former areas, inshore of tidal mixing fronts (cf. Fig. 1, Fig.2 and Fig. F2). Within each study year, individual consistency in habitat use with respect to static and weekly-averaged dynamic environmental indices (range $\overline{\beta}_k$ = 0.61 to 0.80) was significantly greater than the null (Fig. 4). In contrast, habitat use was relatively inconsistent across years, except with respect to standardised SST ($\overline{\beta}_{\mathrm{SST}} = 0.74$), which was significantly more consistent than the null. Individual consistency with respect to monthly dynamic environmental indices also followed the pattern described above (Table E6).

Behavioural repeatability

The repeatability of trip durations, the proportion of U-shaped dives and ARS scale was low ($R_{adj} < 0.07$, Table 1) and not significant, except during 2010, when it was only very marginally so (Table E5). Dive rate was repeatable within 2011 and between 2011 and 2012 but not within

2012. Mean dive depth and mean maximum dive depth were significantly repeatable both across years and within years (R_{adj} 0.21 – 0.38, Table 1).

Trip linearity

Most foraging trips were linear rather than circuitous (population median straightness $\bar{\kappa}$ = 0.85, IQR 0.80 - 0.89; Fig. 3). However, looping trips were occasionally made (e.g. trip 6, Fig. 5a). Trip linearity did not differ significantly between years (GLMM z = -1.23, p = 0.220, n birds = 55, n trips = 492). Birds that made more linear trips were also more consistent in their departure directions in 2010 (correlation between $\hat{\kappa}$ and $\hat{\rho}$: r_s = 0.48, n = 37, p = 0.002), in the depth of foraging areas in 2011 (correlation between $\hat{\kappa}$ and $\hat{\beta}_{\text{depth}}$: r_s = 0.60, n = 20, p = 0.005) and in the NPP of foraging areas in 2012 (correlation between $\hat{\kappa}$ and $\hat{\beta}_{\text{NPP}}$: r_s = 0.57, n = 26, p = 0.003). Excepting these results, we found no other significant correlations between $\hat{\kappa}$ and indices of consistency or repeatability, nor any consistent patterns within or across years (Table E9).

Covariance in different measures of consistency

Within years, individuals that were spatially more consistent were also more consistent with respect to most static and dynamic environmental covariates (Table E10), except for depth, fishing effort and front density in 2010 and depth in 2011. In contrast, we found no significant correlation between spatial and environmental consistency across years (Table E10). There was little correlation between within-individual behavioural repeatability (R'_{adj}) and foraging consistency with respect to space or the environment ($\hat{\rho}$ and $\hat{\beta}$, Table E11). A notable exception was that in some years individuals with more repeatable trip durations were also more consistent

with respect to static environmental indices. In addition, in 2011 (but not 2012) R'_{adj} in either mean or mean maximum dive depth was positively correlated with $\hat{\beta}_{\text{depth}}$. Repeatability in $\delta^{13}C$ in the blood of individuals was not correlated with that of $\delta^{15}N$ (r_s = -0.40, 0.07, 0.59 and -0.17 in 2010, 2011 and 2012 and across years respectively; $p > 0.05$ in all cases, n = 9, 16, 12 and 22). There were no correlations between blood isotope R'_{adj} and within-individual behavioural repeatability or foraging consistency (Table E12).

Effects on body condition

Body mass averaged 2.95 kg (sd = 0.05, n = 66). We obtained full morphometric data from 42 birds. Within this group, body mass varied significantly with tarsus length, culmen length and sex (marginal r^2 = 0.43, Table E13). Females averaged 0.19 kg (95% CI ± 0.09 kg) heavier than males. Residual body mass (RBM) ranged from -0.52 to 0.96 kg (sd = 0.17). Within 2012, RBM was significantly positively related to individual repeatability in trip duration ($F_{1,27}$ = 6.26, r^2 = 0.18, p = 0.019; RBM = -304.6 + 2752.5 x R'_{adj} trip duration). Other than that, we found no relationship between RBM and indices of consistency, repeatability or track straightness, either within or across years (Table E14).

Discussion

Our study shows that northern gannets were individually consistent over three successive breeding seasons in their colony departure directions and coarse to mesoscale (10s km) foraging distribution. To our knowledge this is the first study to test for IFSF across years in seabirds so this phenomenon may be more widespread than hitherto supposed. Indeed, several species of pinniped, which, like seabirds, are wide-ranging marine central-place foragers that target meso-

519 and epipelagic prey, show equivalent long-term behaviours (Bradshaw et al. 2004, Call et al.
520 2008, Baylis et al. 2012). We also found evidence of individual consistency in habitat use with
521 respect to relative SST (rSST) and dietary and behavioural specialisations but these were
522 independent of IFSF. IFSF did not decline over time and was of a similar magnitude within years
523 and across years.
524
525 Mounting loggers on seabirds and handling them repeatedly can raise their temporal and
526 energetic foraging costs (Vandenabeele et al. 2011, Vandenabeele et al. 2012). It is conceivable
527 that this in turn could have led birds in this study to forage in a less exploratory and therefore
528 more repeatable manner than that of the population as a whole. However, in 2010, as part of a
529 parallel study at Bass Rock, we monitored a group of non-instrumented gannets and found that
530 their trip durations were very similar (mean = 23.5 hrs, n = 636 trips from 27 birds, SD = 14.4) to
531 those of the birds we tracked (mean = 23.9 hrs, n = 211 trips from 52 birds, SD = 12.6) (Cleasby
532 et al. in press). Moreover, there is now considerable evidence, collected using a range of
533 technologies to track many species, that IFSF is high within breeding seasons in many seabirds
534 (Weimerskirch 2007, Woo et al. 2008, Patrick et al. 2014). Hence, logger effects are unlikely to
535 have biased our conclusions. Our results, together with evidence that temperate and polar-
536 breeding seabirds forage in relatively predictable environments (Weimerskirch 2007), therefore
537 demand a reappraisal of the view that these seabirds are necessarily highly flexible foragers
538 (Lack 1968). Below we discuss these results in more detail, concentrating on the potential causes
539 and consequences of IFSF in seabirds and other colonial central-place foragers.
540
541 ***Does WSLS foraging cause IFSF?***

For WSLS foraging (Kamil 1983, Davoren et al. 2003) to be an effective strategy, the rate at which birds switch to new foraging areas should match the temporal scale of environmental variability. Previous studies have assumed implicitly that switches to new foraging areas occur frequently enough to be observable at the scale of days or weeks (Irons 1998). This assumption appears valid in some low latitude breeders which forage in oceanic waters (Weimerskirch 2007, Weimerskirch et al. 2010). However, in temperate, polar and neritic habitats prey patches may be less variable, perhaps persisting across years (Davoren et al. 2003). In accordance with the WSLS hypothesis, we found that spatial consistency in gannets was not absolute (population mean < 0.6; Fig. 4) and varied considerably within and among individuals (Fig. 3) due to birds occasionally switching foraging areas, within or between years (Fig. 5b). However, if a WSLS strategy predominated at either temporal scale, IFSF would be expected to decay over time. We found no evidence of this, either over 7 successive foraging trips (i.e. ~ 2 weeks) within breeding seasons or over three successive breeding seasons. Rather, the rate of spatial and directional consistency was similar across years to that within years. Furthermore, though gannets generally travelled directly to foraging areas, birds making more direct trips were no more likely to be consistent with respect to space or environmental indices than those making more circuitous ones. This is difficult to reconcile fully with the hypothesis that gannets anticipate the location of prey prior to departing the colony, switching to more exploratory, circuitous movement patterns only when they encounter poor foraging success (Pettex et al. 2010). Nevertheless, our results do not preclude the possibility that WSLS strategies are matched to longer-term environmental variability. If this were the case, IFSF might break down over periods longer than we observed (~ 2 weeks within years and across 3 years). However, IFSF in pinnipeds and probably some other seabirds persist over decades (Woo et al. 2008, Authier et al. 2012).

Does habitat or dietary specialisation cause IFSF?

Previous studies have shown that $´^{15}N$ and $´^{13}C$ in the blood tissues of gannet chicks from Bass Rock (Kakela et al. 2007) and adults breeding in the Celtic Sea (Votier et al. 2010) collected during a single breeding season were repeatable. Given that $´^{15}N$ increases with the trophic position of prey, this may be regarded as evidence of individual dietary specialisation (Bearhop et al. 2006). However, isotopic ratios reflect not only prey type but also the environment from which they come (Moreno et al. 2011), so repeatability of $´^{15}N$ and $´^{13}C$ in individuals' blood tissues could conceivably arise due to individual spatial consistency. The isotopic signatures of prey items we retrieved from breeding gannets poorly resolved individual prey species. Nevertheless, $´^{15}N$ values in the blood tissues of chick-provisioning gannets were significantly repeatable not only within but across years (Table 1), with little or no dependence on baseline ratios (Table E2). Repeatability in $´^{13}C$ was significant within 2011 and 2012 but not across years (Table 1). Blood tissue $´^{13}C$ showed very little dependence on baseline ratios. This is somewhat surprising, given the assumption in seabird isotopic studies that $´^{13}C$ is strongly dependent on the location from which prey are obtained (Cherel and Hobson 2007). However, the shoaling, mesotrophic fish that gannets from the Bass Rock prey upon (sandeels *Ammodytes* spp, mackerel *Scomber scombrus*, herring *Clupea harengus*, etc.; Table E4) are migratory so there may be some mismatch between their isotopic signatures of that of the local environment in which they are captured.

We sampled blood at an interval of approximately 10 days within each year, so the dietary periods integrated by $RBC_{y,1}$, $SER_{y,1}$ and $SER_{y,2}$ may have overlapped to some extent (Barquete

588 et al. 2013). However, RBC samples collected across years are temporally independent and we
589 controlled for confounding environmental, temporal and intrinsic factors so we are confident that
590 $\acute{}^{15}$N was repeatable at this scale. Our data therefore not only support the supposition that gannets
591 are individual dietary specialists (Kakela et al. 2007, Votier et al. 2010) but also show that
592 specialisations with respect to trophic level persist over multiple breeding seasons.
593
594 Animals with high IFSF also frequently exhibit stereotyped foraging behaviours and habitat
595 preferences (Elliott et al. 2008, Woo et al. 2008, Newsome et al. 2009, Patrick and Weimerskirch
596 2014). However, the relationships between individual consistency in behaviour, diet, habitat use,
597 and space use is complex, and the direction of causality may be unclear (Beverly et al. 2009, Dall
598 et al. 2012). For example, if a prey species are limited to particular locations, IFSF could arise as
599 a consequence of individual dietary specialisations or *vice versa*. We found no evidence of such
600 relationships, indicating that in gannets IFSF and individual dietary specialisation are
601 independent or at most only weakly connected. Alternatively, individual habitat preferences
602 could give rise to IFSF. In our study, individual gannets were consistent with respect to
603 environmental variables within years (see also (Patrick et al. 2014)) and environmental
604 consistency was higher in birds that were more spatially consistent. However, dynamic
605 environmental variables did not differ greatly at the scale of tracking periods within years (i.e. 1
606 – 2 weeks) so this result provides weak evidence for causality. Across years, foraging gannets
607 were also consistent with respect to rSST, which varied markedly (Fig. F2), suggesting that some
608 individuals may track particular stratification regimes, for which rSST is a proxy (Bowers and
609 Simpson 1987). Nevertheless, it is unlikely that individual habitat preferences could account for
610 IFSF because inter-annual IFSF did not correlate with individual consistency with respect to

611 rSST. Moreover, patches of mixed and stratified waters were widely distributed throughout the
612 study area (Fig. F2).
613
614 Within years, gannets with more consistent trip durations were also more consistent with respect
615 to space and static environmental indices. This is most likely because gannet trip durations are
616 proportional to the maximum distance reached from the colony (Hamer et al. 2000). Other links
617 between behavioural repeatability and IFSF were weak or absent. For example, in contrast to a
618 previous study (Patrick et al. 2014), we found very little evidence that dive profiles were
619 repeatable (Table 1; Table E5). Dive rates at Bass Rock within 2011 and across study years, as
620 well as dive depths in all periods, were significantly repeatable. However, there was no
621 relationship between individual repeatability in these behaviours and consistency with respect to
622 spatial, environmental or isotopic consistency. Moreover, the scale of ARS did not differ
623 significantly between individuals. ARS scale may therefore be dependent on factors common to
624 all individuals, such as the scale of prey patches, which is limited by physical processes
625 (Fauchald and Tveraa 2006).
626
627 ***Does site familiarity cause IFSF?***
628 Given the weak evidence to support the hypothesis that IFSF is driven predominantly by other
629 forms of individual consistency or a short-term WSLS strategy, we consider another hypothesis:
630 that foraging site fidelity in gannets results, in part at least, from site familiarity (Irons 1998,
631 Piper 2011). Until recently the role of site familiarity in habitat selection was largely overlooked
632 in favour the ideal free/ideal despotic models, which make the unrealistic assumption that
633 animals are perfectly informed about their environment (Fretwell and Lucas 1969) or models that

634 emphasise the role of information gain from public sources (Ward and Zahavi 1973, Danchin et
635 al. 2001). However, recent habitat selection studies suggest that it may be more advantageous for
636 animals to remain in familiar locations than hitherto supposed (Piper 2011). Indeed, the
637 investment made in site familiarity can explain decisions to remain at relatively poor quality sites
638 (the 'always stay strategy' (Switzer 1993)). During breeding, when energetic demands are high
639 and time constraints severe, foraging in a familiar location may be less risky than exploring more
640 widely (this leads to the testable prediction that IFSF will be higher in breeding birds than in less
641 constrained birds, such as failed breeders). Moreover, remaining in a familiar location may
642 advantage individuals by reducing competition from less well informed conspecifics (Piper
643 2011). By analogy with other forms of individual specialisation, this implies that IFSF may be a
644 density-dependent phenomenon (Araujo et al. 2011).
645
646 Prior to first breeding, immature seabirds prospect at multiple colonies, potentially using public
647 information to assess site quality (Danchin et al. 2001, Votier et al. 2011). This life history stage
648 lasts longer in pelagic seabirds than in most other avian groups, an adaption thought to allow
649 individuals to learn to forage effectively in the marine environment (Lack 1968), but the
650 considerable investment made in the breeding site during this time may also account for the high
651 degree of philopatry in seabirds. Furthermore, the tendency for foraging site familiarity to accrue
652 with age may act to canalise foraging site decisions, to the extent that adult IFSF is high. This
653 process of experience-mediated behavioural canalisation is similar a mechanism hypothesised to
654 explain the phenomenon of wintering site fidelity (*ortstreue*), which is widespread in migratory
655 birds (Alerstam 1990, Guilford et al. 2011).
656

The roles of environmental predictability and behavioural flexibility

A potential cost of IFSF and specialisation is that individuals lack the flexibility to respond to environmental change (Bolnick et al. 2003). Early theories of seabird life history traits and behaviour were founded on the assumption that seabirds forage in such stochastic environments (Lack 1968). For example, the information centre hypothesis posits that seabirds use public information, acquired at the colony, to locate ephemeral prey patches (Ward and Zahavi 1973). Only one study has provided direct support for the information centre hypothesis in seabirds (Weimerskirch et al. 2010) and evidence of short-term IFSF has been regarded as contrary to this hypothesis (Irons 1998). However, indirect evidence suggests that foraging *Morus* spp. exploit both private and public information (Wakefield et al. 2013). At the population-level, gannets from Bass Rock are clearly flexible, both in diet (Table E4, (Hamer et al. 2007)) and range (Fig. 2 and Fig. F1). During our study, individual dietary specialisation and spatial, environmental and behavioural consistency, while significant, were not absolute (Fig. 4). Rather, birds sometimes switched between foraging areas (Fig. 3 and Fig. 5b). A possible explanation is that foraging strategies differ with life history stage, site familiarity and environmental conditions (Piper 2011). Exploratory behaviour, aided by public information, is likely only during immaturity or when foraging success is low (Ward and Zahavi 1973), while the benefits of IFSF are likely to increase with age (Pärt 1995). However, adults may retain flexibility by using a hierarchical strategy. It is notable that some of our study birds were consistent in their departure directions but less so in their foraging areas (Fig. 3). Gannets may therefore be faithful primarily to a directional arc, rather than an area *per se* (Hamer et al. 2001). By departing the colony within this arc they would remain in familiar waters yet have scope to travel further from the colony if foraging success is poor during the early stages of a trip (the ‘trap line’ strategy (Wanless et al.

680 1990)). Only if foraging success was poor throughout the favoured arc would they then switch to
681 another, guided either by memory or the movements of conspecifics from the colony.
682
683 The optimal strategy will also depend on environmental predictability (Switzer 1993). For
684 example, IFSF in lactating New Zealand fur seals (*Arctocephalus forsteri*) is higher in neritic
685 than oceanic waters, which is thought to reflect the degree of predictability in these two habitats
686 (Baylis et al. 2012). Temperate and polar seabirds forage on much more predictable resources
687 than hitherto supposed (Weimerskirch 2007) and there is now abundant evidence that, far from
688 being featureless and stochastic, neritic waters are highly structured by predictable factors, such
689 as bathymetry and the tides (Fig. F2) (Bowers and Simpson 1987, Scott et al. 2010). Our study
690 shows that, at the coarse scale, foraging gannets target individually consistent locations,
691 suggesting that at this scale the occurrence of prey is predictable. At finer scales gannets use
692 ARS and local enhancement to locate their prey (Hamer et al. 2009), implying that the
693 predictability of prey is considerably lower at these scales. This accords with the hierarchical
694 patch model of seabird prey (Fauchald and Tveraa 2006). As such, it is likely that IFSF is scale
695 dependent and declines rapidly below the coarse scale. Foraging ranges during our study were
696 low to intermediate when compared to those recorded at Bass Rock in previous years (Fig. F1).
697 Given that foraging range increases in years of low prey availability (Hamer et al. 2007, Garthe
698 et al. 2011), this suggests that prey were in good supply during our study. Furthermore, we found
699 that environmental variability in the area exploited by Bass Rock gannets was lower across years
700 than that within years during our study (Table E3, Fig. F2), suggesting that the location of prey
701 may have been predictable across years. In years of lower food availability or predictability IFSF
702 may be less marked than we observed.

703

704 Given our evidence of individual IFSF and specialisation with respect to diet, habitat (relative
705 SST) and behaviour (dive rate and mean dive depth) in gannets, it is pertinent to ask whether
706 these traits confer fitness advantages. We found only weak evidence that that residual body mass
707 was dependent upon consistency of foraging behaviour. However, the fitness consequences of
708 IFSF in black-browed albatrosses *Thalassarche melanophris* and southern elephant seals
709 *Mirounga leonina* are only apparent over decadal time scales (Authier et al. 2012, Patrick and
710 Weimerskirch 2014). Ultimately, longer-term tracking, combined with dietary, environmental
711 and demographic monitoring, will be required to determine the persistence, proximate causes and
712 fitness consequences of IFSF in breeding seabirds.

713

714 ***Wider implications***

715 Our study, together with others on pinnipeds, bats and ants, suggests that IFSF may be a trait
716 common to colonial central-place foragers. Increasingly, tracking studies are conducted to
717 estimate the distributions of wide-ranging marine species, such as seabirds and pinnipeds, for
718 conservation purposes. If IFSF is widespread in this group, the implication is that research
719 resources would be better directed to tracking many individuals for short representative periods
720 in the life history stages of interest, rather than fewer individuals for longer. However, resource
721 selection models fitted to such data generally make the implicit assumptions that foragers are
722 perfectly informed about their environment and select the most favourable habitats (Fretwell and
723 Lucas 1969) but the effects of site familiarity and fidelity, as well as dietary and habitat
724 specialisation are rarely considered (Piper 2011, Dall et al. 2012). As a consequence, such
725 models may over-predict the degree to which animals track spatiotemporally patchy resources.

726 Indeed, long-term strategies that give rise to IFSF may account for the observation that at shorter
727 time scales there is frequently a mismatch between the coarse-scale distribution of seabirds and
728 their prey (Grémillet et al. 2008, Fauchald et al. 2011). It is frequently suggested that seabirds
729 and other higher predators, such as pinnipeds, can be used to monitor the state of the marine
730 environment (Boyd et al. 2006), yet the tendency for IFSF and dietary specialisation to weaken
731 the link between predator demography and short-term environmental variability implies that this
732 may be less fruitful than otherwise supposed. Importantly, if IFSF does arise through site
733 familiarity, this implies that environmental conditions experienced during development may
734 have lifetime consequences (Dall et al. 2012). Moreover, rapid climate change may have an
735 unexpected cost on seabirds if their life history strategy is reliant on the veracity of site-specific
736 information gained early in their long lives (Hipfner 2008). Given this and the many other
737 potential implications of IFSF and specialisation in colonial central-place foragers (Bradshaw et
738 al. 2004, Weimerskirch 2007, Call et al. 2008) we urge that long term longitudinal tracking
739 studies be employed to test for these phenomena and alternative explanatory hypotheses in other
740 members of this group.
741

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748

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Supplemental Material

Appendix A.

Sources and pre-processing of environmental data used in the analysis.

Appendix B.

Additional description of the methods used to determine gannet tissue and environmental baseline stable isotope ratios.

Appendix C.

Additional description of methods used to quantify and classify the behaviour of gannets at sea.

Appendix D.

Illustration of individual foraging consistency indices using contrasting examples.

Appendix E.

Additional results tables, including details on sample sizes; foraging models; environmental variability; diet; individual repeatability and consistency; correlations among behavioural and dietary indices; morphology and its dependence on behavioural and isotopic repeatability.

Appendix F.

Additional results figures, including inter-annual variation in foraging range; dynamic environmental conditions during the study; static environmental covariates considered; prey and gannet blood stable isotope ratios; all tracks of gannets foraging from Bass Rock; and directional and spatial consistency across successive trips within years.

987 **Table 1.** Repeatability (R_{adj}) of foraging behaviour and blood stable isotope ratios in chick-

988 provisioning gannets†.

Statistic	R_{adj}			
	Within 2010	Within 2011	Within 2012	Across years
´ ^{15}N	**0.20**	**0.35**	**0.35**	**0.33**
´ ^{13}C	**0.37**	**0.55**	0.18	0.03
Trip duration	0.04	0.02	0.01	0.01
ARS scale	0.01	0.01	0.02	0.02
Dive rate	-	**0.50**	0.04	**0.43**
Proportion U-shaped dives	-	**0.07**	0.00	0.00
Mean dive depth	-	**0.38**	**0.37**	**0.36**
Mean max dive depth	-	**0.37**	**0.29**	**0.21**

989 Values in **bold** are significant based on 95% credible intervals (Table E5).

990 † For sample sizes see Table E2.

991

992

Figure legends

Fig. 1. Study area, showing (**a**) depth (25 m contours), Bass Rock (yellow triangle) and other locations mentioned in the text: 1. Moray Firth; 2. NE Scotland coastal waters; 3. Farnes Deep, 4. Dogger Bank. (**b**) Average summertime SST, 2010 – 2012. The 13 °C isotherms in July 2010, 2011 and 2012 (blue, red and black lines respectively) indicate the approximate interface between mixed and stratified waters in those years. Dashed lines show 100 km intervals of distance-by-sea from Bass Rock.

Fig. 2. Foraging distribution of chick-provisioning northern gannets tracked from Bass Rock during June-August, 2010, 2011 and 2012. UD = mean foraging Utilisation Distribution estimated using the first 3 trips recorded from each individual tracked for e 3 trips in each year (37, 20 and 31 birds respectively). Smoothing parameter h = 15 km. Dashed lines indicate 100 km intervals of distance-by-sea from Bass Rock (yellow triangle).

Fig. 3. The first track of chick-rearing gannets recorded in each year (red = 2010; blue = 2011; green = 2012). Panels corresponding to each bird (identity bottom right) are arranged in descending order of spatial consistency across years ($\overline{\beta}'_{x,y}$). Birds illustrated were tracked for e 1 trip in each study year (for the full dataset see Fig. F5). Dashed lines show 100 km intervals from Bass Rock. $\overline{\rho}$ = directional consistency across years.

Fig. 4. Mean consistency of gannets over three foraging trips (coloured symbols) compared to the null distribution expectation (5^{th}, 25^{th}, 75^{th} and 95^{th} percentiles) determined by randomly

reassigning bird identity to tracks 999 times without replacement (see Table E6 for details). Colours and symbols indicate the probability that mean consistency is significantly greater than the null. x, y = Cartesian space; SST = sea surface temperature; FD = front density; NPP = net primary production. Dynamic environmental covariates were averaged by week prior to analysis.

Fig. 5. Most gannets were consistent in their colony departure directions and foraging locations (e.g. **a**). However, a minority were largely inconsistent (e.g. **b**). Numbers indicate terminal locations of successive trips in 2010 (colours grade from red to blue with time). Yellow triangle = Bass Rock.